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Authors: Rogerson, Jared D., Fairbanks, W. Sue, and Cornicelli, Louis

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ECOLOGY OF GASTROPOD AND BIGHORN SHEEP HOSTS OF LUNGWORM ON ISOLATED, SEMIARID MOUNTAIN RANGES IN UTAH, USA

Jared D. Rogerson,[1,3] W. Sue Fairbanks,[1,4,6] and Louis Cornicelli[2,5]

[1] Department of Biology, University of Nebraska at Omaha, Omaha, Nebraska, 68182, USA
[2] Utah Division of Wildlife Resources, 515 E 5300 S, Ogden, Utah 84405, USA
[3] Current address: Wyoming Game and Fish Department, 117 S. Sublette Ave., Pinedale, Wyoming 82941, USA
[4] Current address: Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011, USA
[5] Current address: Minnesota Department of Natural Resources, 500 W. Lafayette Blvd., St. Paul, Minnesota 55155, USA
[6] Corresponding author (email: suef@iastate.edu)

ABSTRACT: Isolated, nonmigratory populations of bighorn sheep (*Ovis canadensis*) may experience high exposure to lungworms (*Protostrongylus* spp.) through a build-up of fecal material. However, semiarid climates may hinder lungworm transmission by limiting terrestrial gastropods, the intermediate hosts. We assessed potential for lungworm transmission, documented occurrence of transmission, and identified habitat types where transmission was likely to occur on ranges of two recently introduced populations of bighorn sheep in northern Utah. Gastropods were collected weekly on Antelope Island and the Newfoundland Mountains, May–August 2001–02, from each of the four major habitat types (riparian, rock, desert shrub, and grass). Distribution of 113 bighorn sheep groups was observed, and 421 fecal pellet groups were collected to estimate lungworm levels. A total of 1,595 gastropods representing five genera were collected from both ranges. *Vallonia* made up 85% of all gastropods collected. Of 980 gastropods collected on Antelope Island in 2002, only *Vallonia* were found infected with protostrongylid-type larvae (10 of 980=1%). Lungworm prevalence in bighorn fecal samples was 97% on Antelope Island and 90% on the Newfoundland Mountains. Lungworm prevalence in lambs indicated lungworm transmission was occurring on Antelope Island. Lungworm transmission was likely occurring in riparian habitat due to abundant gastropods, presence of infected gastropods, and reliance by bighorn sheep on few water sources. Differences in spatial distribution between ram and nursery groups may partly explain higher fecal larvae counts in nursery than in ram groups. We suggest lungworm levels in bighorn sheep on semiarid ranges may increase in dry years as bighorn sheep concentrate use on fewer perennial water sources.

Key words: Antelope Island, bighorn sheep, gastropod, intermediate host, lungworm, Newfoundland Mountains, *Ovis canadensis*, *Protostrongylus* spp.

INTRODUCTION

The lungworms *Protostrongylus stilesi* and *Protostrongylus rushi* are endemic inhabitants of bighorn sheep lungs, and high prevalence of these parasites in bighorn populations is common (Forrester, 1971; Kistner et al., 1977; Festa-Bianchet, 1991a). If increased immune response to heavy lungworm infections leads to a decrease in Th1 immune responses to other pathogens (Kullberg et al., 1992; Actor et al., 1993; Abbas et al., 1996), lungworm infections may play an important role in susceptibility of bighorn sheep to viral and certain other diseases. In addition, evidence that parasite resistance is energetically costly (Festa-Bianchet, 1989; Pelletier et al., 2005), and that nematode parasites in domestic sheep can play a role in weight gain and mortality (Gulland, 1992; Wilson et al., 2004), indicates that increased understanding of the relationships between the parasite and its intermediate and definitive hosts is an important management issue. Lungworms may be of particular management concern in isolated, nonmigratory bighorn populations, where constant reinfection may lead to high parasite loads (Jones and Worley, 1997).

Transmission of the lungworm parasite is dependent on overlap in temporal and spatial distribution of intermediate hosts and bighorn sheep. Few studies have directly investigated the link between the

ecology of the intermediate hosts and definitive hosts of the lungworms of bighorn sheep. Based on distribution and abundance of gastropod intermediate hosts and migratory and foraging behavior of bighorn sheep, aspen copses and grassy openings were identified as likely habitats for lungworm transmission in fall and spring, respectively, on a bighorn sheep winter range in Alberta (Boag and Wishart, 1982; Robb and Samuel, 1990). On the other hand, the limiting effects of desert environments on gastropods may explain low levels of lungworms in desert bighorn sheep (*O. c. nelsoni*) (Clark et al., 1985). The importance of different habitats and the timing of lungworm transmission are likely to differ among regions. In addition, spatial segregation of the sexes outside the breeding season (Mysterud, 2000; Bowyer, 2004) may lead to differences in exposure of male and female bighorn sheep to infected intermediate hosts in different habitats.

Our study addressed aspects of lungworm transmission on isolated, semiarid ranges by focusing on the ecology of both intermediate hosts and bighorn sheep. California bighorn sheep (*O. c. californiana*) were introduced to Antelope Island and the Newfoundland Mountains in northwestern Utah in 1997 and 2001, respectively. Both locations are isolated from other mountain ranges, one by the Great Salt Lake and the other by wide expanses of salt-flat desert. Furthermore, bighorn sheep populations are restricted to using only a portion of their respective ranges: by availability of suitable habitat on Antelope Island, and by availability of water in summer on the Newfoundland Mountains. Consequently, amplified rates of lungworm transmission might be expected because of limited distribution of the bighorn sheep. Conversely, the semiarid climate in which they exist may hinder transmission through limitations on gastropods.

The goal of our study was to gain an understanding of the ecological relationships between intermediate and definitive hosts of lungworms in isolated, semiarid mountain ranges. Specific objectives were to 1) determine the distribution and abundance of terrestrial gastropods that might serve as intermediate hosts, 2) determine whether transmission was occurring on these two ranges by assessing larval lungworm prevalence and counts in bighorn fecal pellets, and 3) identify habitats in which lungworm transmission was likely to occur by comparing location of infected gastropods with sex-specific distribution of bighorn sheep.

If lungworm transmission to bighorn sheep was occurring, we expected to find lungworm infection in lambs. We also expected lungworm prevalence in gastropods to be greatest in locations with the most overlap in distribution of gastropods and bighorn sheep. The results of this research will assist in predicting the potential for lungworm-related problems in this and future reintroduction efforts and may also provide the basis for development of management strategies for controlling lungworms in semiarid environments.

MATERIALS AND METHODS

Study areas

Antelope Island (40°95′N, 112°21′W) is a 10,409-ha island located in the Great Salt Lake in northern Utah (Davis County). This semiarid grassland has an average annual temperature of 17.5 C and receives an average of 45.6 cm of precipitation annually (Western Regional Climate Center). Elevation ranges from 1,280 to 2,011 m, and areas of steep, rocky terrain suitable as bighorn habitat are limited. Eighty ephemeral and perennial springs have been reported (Mayo and Klauk, 1991), but probably only a few of these are important to the bighorn sheep based on their location in relation to bighorn sheep habitat. Twenty-three California bighorn sheep were introduced to the island in 1997, and the population reached a size of about 125 individuals by 2002.

The Newfoundland Mountains (41°14′N, 113°22′W) are located about 80 km west of Antelope Island in the Great Salt Lake Desert (Box Elder County). It is a 17,352-ha, semiarid

to arid, rocky "island" completely surrounded by desert salt flat rather than water. Average annual temperature on the Newfoundland Mountains is 18.5 C with an average of 27.0 cm of annual precipitation (Western Regional Climate Center). Elevation ranges from 1,288 m to 2,135 m. Water availability is limited to the northern third of the range. At least 16 water sources were present, with four estimated as reliable perennial springs. Thirty-one California bighorn sheep were released onto the Newfoundland Mountains in 2001, 15 of which were taken from Antelope Island. The population was estimated at about 40 animals by 2002.

There is no strong evidence that bighorn sheep inhabited Antelope Island or the Newfoundland Mountains in recent history, although bighorn sheep did occur on surrounding mountain ranges. Therefore, these ranges were considered to be free of lungworms (*Protostrongylus* spp.) at the time of bighorn sheep introduction. Domestic sheep had been absent from Antelope Island for 50 yr, and for 6 yr on the Newfoundland Mountains, prior to the bighorn sheep introductions. Therefore, the occurrence of *Muellerius capillaris*, a lungworm commonly found in domestic sheep that can infect bighorn sheep (Pybus and Shave, 1984), was not expected. All bighorn sheep were treated with one subcutaneous injection of Ivermectin prior to release as part of standard protocol in an attempt to reduce intensity of lungworm infection.

Collection of gastropods

Terrestrial gastropods were sampled from mid-May through mid-August 2001–02. Three different methods were used to account for effects of weather on sampling techniques and the degree of bias involved (Boag, 1982, 1990; Hawkins et al., 1998), and potential ecological differences among gastropods (Bishop, 1977; Hawkins et al., 1998). The primary method of collecting gastropods was with permanent-plot transects (Boag, 1982) located within range used by bighorn sheep. Areas of use were based on 1998–2000 bighorn sheep habitat use on Antelope Island (Hill, 2002). At each study area, three 30-m transects were established in each of four major habitat types: rock, grass, desert shrub, and riparian. Rock habitat included rock outcrops, boulders, and talus. The major grasses on both ranges included bluebunch wheatgrass (*Agropyron spicatum*), cheatgrass (*Bromus tectorum*), sand dropseed (*Sporobolus cryptandrus*), and purple threeawn (*Aristida purpurea*) (Hill, 2002; pers. obs.). Dominant shrubs in desert shrub habitat were big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus viscidiflorus*), saltbush (*Atriplex* spp.), and broom snakeweed (*Gutierrezia sarothrae*). The lush green vegetation surrounding a water source (primarily springs) was considered riparian habitat. Trees occurred in some riparian areas, but were rare on both ranges. At 5-m intervals along each transect, a 30×30×1.91-cm plywood square was placed on the ground over a 30×30-cm square of corrugated cardboard. In rock habitat, transects were placed in narrow areas between rock outcrops or through boulder fields such that the plots were contacting soil or sparse vegetation. The evening before collection, the area beneath each plot was moistened with 1 l of water, creating a favorable microclimate for gastropods. The next morning gastropods on, or immediately beneath, the plots were collected. Gastropods were usually collected from permanent-plot transects on a weekly basis and used to calculate the mean number of gastropods collected per plot for each transect. Because this collection method influences both vertical and horizontal movement of gastropods (Boag, 1990; Hawkins et al., 1998), it is not an accurate method of estimating gastropod densities, and we did not calculate actual densities. In 2001 permanent-plot transects were visited between 11 and 13 times on Antelope Island and between nine and 13 times (67% ≥11 visits) in the Newfoundland Mountains. In 2002 permanent-plot transects were sampled 11 times on each study area.

In addition, three 15-m temporary transects per habitat type, parallel to permanent-plot transects and at a random distance between 1 and 10 m, were chosen biweekly. Vegetation was searched for gastropods and shells in 30×30-cm quadrats placed at 5-m intervals along transects. A third sampling method, soil sifting, also employed these temporary transects. After searching vegetation, one quadrat per habitat type was randomly chosen and a 30×30×6-cm soil sample was taken and later sifted through fiberglass screening with 1.0×1.4-mm mesh for gastropod or shell removal. An average of 15 (2001) and 13 (2002) transects per habitat type were established for vegetation/soil searches on Antelope Island. On the Newfoundland Mountains, 15 transects per habitat type were searched in 2001, with an average of 16 per habitat type in 2002. Because so few live gastropods were collected using the soil sifting method in 2001 (12 gastropods; 11 on Antelope Island, 1 on

Newfoundland Mountains), this method was not repeated in 2002.

When possible, live gastropods or shells were identified to genus (Burch and Pearce, 1990). Genus identifications were confirmed at the University of Michigan Museum of Zoology. Analyses of gastropod distribution and abundance were based on the combined dataset of all live gastropods collected using all three methods (Boag and Wishart, 1982).

Determination of gastropod infection status

All gastropods collected in 2002 were examined for lungworm larvae. Gastropods were stored in plastic vials and refrigerated (15 C) for a maximum of 1 wk. We then crushed the gastropods between glass slides to spread the snail tissue for examination under a microscope at 25×. Number and developmental stage of protostrongylid-type larvae were recorded. Protostrongylid-type larvae were identified on the basis of length, presence of a symmetrically tapered, pointed posterior end, and the presence or absence of a dorsal spine (Robb and Samuel, 1990). Third-stage larvae (L_3) were identified as infective based on the presence of a darkened cuticle (Monson and Post, 1972; Samson et al., 1987), and the other developmental stages were recorded as uninfective. It is unlikely that *Protostrongylus boughtoni* was present, as there were no snowshoe hares (*Lepus americanus*) on the study sites. However, mule deer (*Odocoileus hemionus*) occurred on both ranges, leading to the possibility that *Orthostrongylus macrotis* or *Parelaphostrongylus odocoilei* larvae might be present in gastropods. A dorsal spine distinguishes *Parelaphostrongylus odocoilei* larvae from *P. rushi*, *P. stilesi*, and *O. macrotis* larvae (Ballantyne and Samuel, 1984). However, overlap in the lengths of *P. rushi*, *P. stilesi*, and *O. macrotis* (Kralka and Samuel, 1984) prevented us from distinguishing among these three species in gastropod intermediate hosts.

Bighorn sheep distribution and fecal analysis

Radiocollars still functioning from the introduction onto Antelope Island (10 collars), and 12 collars deployed by the Utah Division of Wildlife on bighorn sheep released on the Newfoundland Mountains were used to locate groups of bighorn sheep weekly from mid-May through mid-August 2001–02. Observations of bighorn groups were also made opportunistically during radiotracking and during gastropod collection. For all groups of bighorn sheep encountered, group composition and age-class were determined. Group type was recorded as either ram or nursery. Ram groups were composed of only males of any age category. Nursery groups contained mostly females and their lambs, but often young rams (≤2 yr) as well, which typically have not begun segregating from ewes (Festa-Bianchet, 1991b). Habitat type in which each bighorn sheep group was observed was identified as riparian, rock, desert shrub, or grass. Location of each group was either plotted on U.S. Geological Survey topographic maps (1:7,500) in the field and later converted to Universal Transverse Mercators (UTM) or determined with a global positioning system (GPS; Garmin International, Olathe, Kansas, USA).

In this study we used fecal larvae counts to investigate lungworm transmission in introduced bighorn populations and the ecological relationships between the intermediate and definitive hosts. Conducting counts of lungworms in bighorn sheep fecal pellets is a useful tool in determining if transmission is occurring on the ranges. The presence of lungworm larvae in lamb feces provides evidence for transmission, regardless of whether they acquired them transplacentally or orally. Only L_3 larvae are infective to bighorn sheep, and therefore larval development must have taken place in an intermediate host gastropod. In the event of transplacental transmission, L_3 lungworms ingested by the ewe are held in the lungs for a time (rather than developing to the adult stage) and later passed to the fetus (Hibler et al., 1982). Based on experimental infections of captive bighorn lambs, the prepatent period of *P. stilesi*, in combination with *P. rushi* or not, was between 43 and 54 days (Fougere-Tower and Onderka, 1988). It is likely that L_3 larvae that pass through the placenta and are already established in the lung of neonates may develop into adult worms and produce L_1 larvae sooner than larvae that are ingested by lambs. Additionally, lambs may become infected by ingesting infected gastropods.

Fecal counts of parasite larvae constitute an indirect measure of infection intensity, which usually have an unknown relationship to the actual number of parasites infecting a host (Wilson et al., 2002). Lungworm larval output in bighorn sheep feces may be related to infection intensity (Forrester and Senger, 1964; Uhazy et al., 1973), but is also likely to be influenced by a variety of other factors, such as the immune response of the host or density-dependence of parasite fecundity (Festa-Bianchet, 1991a; Wilson et al., 2002). Although sensitivity of indirect measures to detect prevalence may be low (Wilson et al., 2002), repeated sampling of known bighorn

sheep revealed few false-negatives using fecal counts of lungworm larvae (Festa-Bianchet, 1991a). The high variability of fecal larvae counts may obscure differences between groups of individuals (Wilson et al., 2002), making it difficult to interpret negative results. Despite these methodological problems, field studies have relied on these noninvasive, indirect measures to investigate parasitism and its relationship to population and behavioral ecology, particularly in wild ungulate populations (Festa-Bianchet, 1989; Goldstein et al., 2005; Pelletier et al., 2005; Acevedo et al., 2005).

Entire fecal pellet groups from individuals of ram and nursery groups were collected by observing animals until they defecated. Emphasis was placed on collecting fresh fecal pellets because, in the presence of precipitation, lungworms may become activated and exit feces in search of intermediate host gastropods (Forrester, 1971). Hot, dry conditions may reduce the number of viable lungworm larvae in feces through desiccation, although protostrongylid larvae seem quite tolerant (Forrester and Senger, 1963; Solomon et al., 1998). Using only fresh feces ensured more accurate assessment of fecal output of lungworm larvae. However, due to difficulty of visually observing bighorn groups on the Newfoundland Mountains and the small amount of precipitation the range receives, all fecal pellets that did not appear weathered were collected. These samples were defined as "old." Pellets were identified as belonging to ram, nursery, or lamb fecal categories. Fecal pellets from lambs were easily identified based on pellet size and were thus examined separately from nursery groups in all statistical analyses. In some analyses counts of fecal pellets from adults of unknown group types were included with pellets from ram and nursery groups in an "adult" category.

As lungworm levels in bighorn sheep feces are reported, in many areas, to be highest in late winter/early spring (Samson et al., 1987; Festa-Bianchet, 1991a; Goldstein et al., 2005), we also collected fecal pellets in March 2002 from Antelope Island. The March fecal samples were included in the overall analysis of lungworm prevalence on Antelope Island. Thus, we make the assumption that *prevalence* of lungworm larvae in fecal pellets does not change substantially between the months of March and August.

Fecal pellets were allowed to air dry in paper sacks and lungworms were extracted using the modified Baermann-beaker method (Forrester and Lankester, 1997a, 1997b). Fecal samples from both ranges were handled in the same manner, and lungworm extraction in the lab began in October of the same year in which fecal samples were collected. To aid in counting, the petri dish was placed over a grid with 3.5×3.5-mm squares. One half of the petri dish was randomly selected and examined under stereoscopic magnification at 20×. First-stage lungworm larvae (L_1) were identified to genus and counted to estimate the number of lungworm larvae per gram of dried feces (LPG). In the event that no lungworms were observed, the other half of the petri dish was searched to confirm absence of larvae.

Data analysis

G-tests (Zar, 1996) were used to compare relative abundances of gastropod species between years, the distribution of gastropods among habitat types, and between ranges and years, and to compare distribution and abundance of gastropods with distribution of bighorn sheep. Relative abundance was used because, although gastropod capture effort was identical on the two ranges and across habitat types in 2002 and nearly so in 2001, total gastropods collected on Antelope Island were much higher than on the Newfoundland Mountains in both years. Also, our primary collection method (permanent-plot transects) may not be an accurate estimate of gastropod density, because creation of suitable microclimates under the plots affects horizontal and vertical movement of gastropods (Boag, 1990; Hawkins et al., 1998). Prevalence of lungworm infection in intermediate hosts was calculated as the percentage of the total gastropods collected in 2002 that were infected with protostrongylid-type larvae.

Prevalence of lungworm infection, as indicated by the proportion of bighorn sheep fecal samples containing L_1 larvae, was determined for each population in each year. Difference in lungworm prevalence between bighorn populations was determined with a test of two proportions. In most cases attempts to achieve normality or homogeneity of variances of fecal larvae counts through data transformation were unsuccessful. Therefore, median larvae counts, based on all fresh fecal samples, are reported, and nonparametric statistics were used for comparisons. Median larvae counts are based on fecal samples collected May through August in each year. Although larval output in bighorn feces differs significantly between late winter/early spring and summer/fall (Uhazy et al., 1973; Goldstein et al., 2005), variation in fecal larvae counts between May and October was not significant (Uhazy et al., 1973). However, reported

seasonal patterns differ among populations (Arnett et al., 1993); therefore, we tested for variation in fecal larvae counts among months (May–August) in each year. Kruskal-Wallis H test was used to examine differences in median larvae counts among ram, nursery, and lamb fecal counts within each range and between years. We used Mann-Whitney U tests to determine location of significant differences. Differences in distribution between ram and nursery groups on each range were analyzed with G-tests.

The distribution of larvae counts across fecal samples was described using a corrected moment estimate of the parameter k from a negative binomial distribution (Elliot, 1977), for fecal samples from rams and from nursery groups (excluding lambs) from Antelope Island. Because there were fewer fecal samples collected on the Newfoundland Mountains, k was calculated for all adults combined. A k greater than about 20 suggests a random distribution across samples, while k values of ≤ 1 represent a highly aggregated distribution (Wilson et al., 2002).

RESULTS

Bighorn sheep fecal analysis

A total of 392 bighorn sheep fecal samples collected from Antelope Island ($n=299$ fresh) and the Newfoundland Mountains ($n=60$ fresh, $n=33$ old) during May–August 2001–02 was used to estimate prevalence of protostrongylid-type larvae and fecal larvae counts. On the Newfoundland Mountains, old fecal samples were not included in calculating prevalence, but were used in calculating median larvae counts for adult bighorn sheep. Including old samples testing positive for lungworms increased sample size without significantly changing the median larvae count. Fecal larvae counts for 29 additional fecal samples (10 ram, 19 unknown) collected on Antelope Island in March 2002 were analyzed separately.

Prevalence of lungworms in fecal samples from adult bighorn sheep was greater on Antelope Island (97%, $n=275$) than the Newfoundland Mountains (90%, $n=48$) ($z=2.76$, $P=0.006$). On Antelope Island, lungworm prevalence in feces was 98% ($n=155$) for samples from nursery groups, 97% ($n=101$) for samples from ram groups, and 87% ($n=23$) for lamb fecal samples. Lambing occurred on Antelope Island from early April through mid-June. Lamb fecal samples were collected between 21 May and 2 July in 2001, and two of six (33%) lamb pellet groups collected on 21 May were negative for lungworm larvae. In 2002, lamb pellet groups were collected 29 May–17 July, and the only pellet group in which lungworm larvae were not detected was collected on 17 July.

On the Newfoundland Mountains, lungworm larvae were present in 92% ($n=24$) of samples from ram groups and 84% ($n=19$) of nursery group fecal samples. Only two lamb fecal samples were collected from this population in 2001; one sample collected 21 June contained lungworms, one collected 25 July did not. In 2002, all 10 lamb fecal samples from the Newfoundland Mountains, collected 29 July–5 August, were lungworm-free.

Median larvae count during May–August for all adult fecal samples combined on Antelope Island ($\text{median}_{2001}=171$ LPG, $\text{median}_{2002}=88$ LPG) was significantly higher than for adults on the Newfoundland Mountains in both years ($\text{median}_{2001}=13$ LPG, $\text{median}_{2002}=24$ LPG; $U_{2001}=23{,}593$, $P<0.001$; $U_{2002}=6{,}632$, $P=0.0001$). Median larvae count did not differ by month collected (May–August) on Antelope Island in 2001 (Kruskal-Wallis test: $H=4.59$, $P=0.20$) or in 2002 ($H=3.68$, $P=0.30$); sample size of fecal pellets on the Newfoundland Mountains was too small to test differences by month. There was a significant decrease in larvae counts in adult fecal samples from Antelope Island between summer 2001 to summer 2002 ($U=27{,}895$, $P=0.010$). Median larvae count for fecal samples collected in March 2002 (median=303 LPG, range=0–674) was higher than for either summer, although not significantly so ($U_{2001}=19{,}740$, $P=0.97$; $U_{2002}=2{,}831$, $P=0.39$), likely due to the small sample size for March. On the Newfoundland

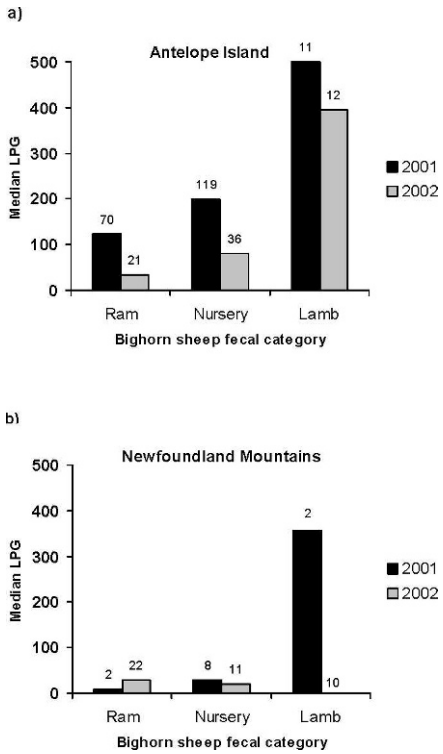

FIGURE 1. Median first-stage lungworm larvae per gram of dried feces (LPG) for fecal samples collected from adult bighorn sheep in ram and nursery groups and from lambs on a) Antelope Island and b) the Newfoundland Mountains, May–August 2001 and 2002. Sample size is given above the bars.

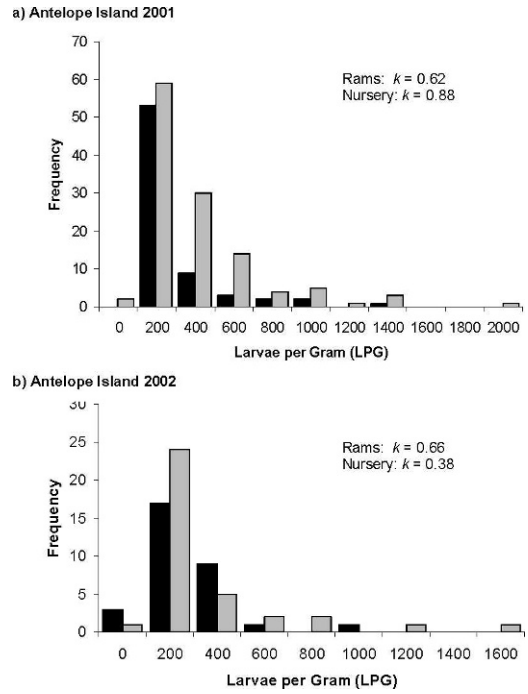

FIGURE 2. Frequency of fecal samples from ram and nursery groups on Antelope Island with different levels of lungworm larvae per gram (LPG) in a) 2001 and b) 2002. k = the corrected moment estimate of parasite aggregation. Black bars = ram groups; gray bars = nursery groups.

Mountains, larvae counts from adult fecal samples did not differ between years (U=1,296, P=0.58). Larvae counts for lamb feces decreased from 2001 to 2002 in samples taken from Antelope Island (Fig. 1a), but the change was not significant (U=153, P=0.21). On the Newfoundland Mountains, the one positive fecal sample from a lamb in 2001 contained 717 LPG, and all tested negative for lungworms in 2002.

On Antelope Island, fecal larvae counts in 2001 differed significantly (H=14.44, P=0.001) among lambs, nursery groups, and ram groups (Fig. 1a). Nursery group values (range=0–1,823) were significantly greater than those for ram groups (range=1–1,318; U=5,523, P=0.002), and values for lamb feces (range=0–3,592) were significantly higher than those for both ram groups (U=659, P=0.004) and nursery groups (U=1,021, P=0.012). In 2002, however, the differences in larvae counts among nursery group (range=0–1,488), ram group (range=0–358), and lamb (range=0–938) fecal categories were not statistically significant (H=3.62, P=0.16). A high degree of aggregation was observed with respect to fecal larvae counts in adult bighorn sheep (Fig. 2).

On the Newfoundland Mountains, no statistical difference was apparent between years for combined adult fecal larvae counts (U=1,295, P=0.58; Fig. 1b). The differences in values among ram (range=4–15), nursery (range=0–96), and lamb (range=0–717) fecal categories in 2001 were not statistically significant (H=0.42, P=0.81). In addition, there was no significant difference between ram (range=0–123) and nursery group (range=0–118) larvae counts in 2002

TABLE 1. Mean (±SE) number of gastropods per plot by species from permanent-plot transects sampled May–August 2001 and 2002 in four major habitat types on Antelope Island and the Newfoundland Mountains.

	Year	Total collected	Habitat type			
			Riparian	Rock	Desert shrub	Grass
Antelope Island[a]						
Vallonia	2001	260	1.32 (0.32)	0	0	0.01 (0.01)
	2002	781	3.32 (0.60)	0.06 (0.04)	0.004 (0.004)	0
Pupilla	2001	3	0	0.02 (0.01)	0	0
	2002	4	0	0.02 (0.01)	0	0
Oreohelix	2001	1	0	0.01 (0.01)	0	0
	2002	1	0	0.004 (0.004)	0	0
Catinella	2001	4	0.02 (0.01)	0	0	0
	2002	181	0.78 (0.23)	0.01 (0.01)	0	0
Unidentified slug	2001	28	0.15 (0.07)	0	0	0
	2002	3	0.01 (0.01)	0	0	0
All gastropods	2001	296	1.53 (0.32)	0.02 (0.01)	0	0.01 (0.01)
	2002	970	4.10 (0.64)	0.09 (0.04)	0.004 (0.004)	0
Newfoundland Mtns[b]						
Vallonia	2001	47	0.15 (0.06)	0.17 (0.08)	0	0
	2002	212	0.56 (0.16)	0.21 (0.10)	0.02 (0.02)	0.13 (0.06)

[a] Transects visited 11–13 times in 2001; 11 times in 2002.

[b] Transects visited 9–13 times in 2001; 11 times in 2002.

($U=401$, $P=0.31$). Estimated aggregation of fecal larvae counts on the Newfoundland Mountains was high (2001: $k=0.60$; 2002: $k=0.36$).

Gastropod collections

During the initial three weeks of sampling in 2001, gastropods were not present under permanent plots. Increased presence of gastropods under permanent plots after the first period of collecting in the initial sampling year may be caused by weathering effects on the plywood plots acting to increase plot acceptability or decrease unanticipated repellent attributes of the plots themselves (Boag, 1990). To eliminate this problem as a confounding factor, the first three weeks of data in 2001 from permanent-plot transects were not included in the analyses.

A total of 1,595 live gastropods were collected in 2001 and 2002 using all three collection methods; 1,315 from Antelope Island and 280 from the Newfoundland Mountains. Snails were identified as belonging to the families Succineidae, Thysanophoridae, Pupillidae, and Valloniidae. Species richness was greater on Antelope Island (six species) than the Newfoundland Mountains (two species). On Antelope Island, five snail species from the genera *Catinella*, *Oreohelix*, *Pupilla*, *Vallonia*, and one unidentified slug species were collected from the permanent-plot transects (Table 1). In addition, three shells of an unidentified snail species were collected from riparian habitat on Antelope Island, but no live specimens were found. Therefore, this unknown species was not included in analyses. On the Newfoundland Mountains, only *Vallonia* and an unidentified pupillid snail were collected using all three formal collection methods (Tables 1 and 2). However, *Oreohelix* was often encountered, both shells and live animals, through casual observation in extremely rocky terrain. On both study areas, the permanent-plot transects yielded the majority of gastropods collected. Further analyses are based on the combined dataset of live gastropods from all three methods.

Vallonia was the most common gastro-

TABLE 2. Total number of live gastropods collected using vegetation search and soil sifting methods combined May–August 2001, and by vegetation search in 2002 in four major habitat types on Antelope Island and the Newfoundland Mountains.

			Habitat type			
	Year	Total collected	Riparian	Rock	Desert shrub	Grass
Antelope Island						
Vallonia	2001	27	27	0	0	0
	2002	8	8	0	0	0
Pupilla	2001	1	0	1	0	0
	2002	0	0	0	0	0
Oreohelix	2001	8	0	8	0	0
	2002	1	0	0	0	1
Catinella	2001	3	1	2	0	0
	2002	1	1	0	0	0
All gastropods	2001	39	28	11	0	0
	2002	10	9	0	0	1
Newfoundland Mtns						
Vallonia	2001	6	5	0	1	0
	2002	11	1	7	2	1
Pupillidae	2001	0	0	0	0	0
	2002	4	0	4	0	0
All gastropods	2001	6	5	0	1	0
	2002	15	1	11	2	1

pod on both study areas in both years using all collection methods (Tables 1 and 2). However, the relative abundance of several of the less common gastropods differed between years on Antelope Island ($G=145.29$, $P<0.001$). In particular, the relative abundance of *Catinella* increased in 2002, while the relative abundance of *Oreohelix* and the slug decreased.

The distribution of gastropods across habitat types differed between ranges in 2001 ($G=257.0$, $P<0.001$) and 2002 ($G=502.4$, $P<0.001$), with gastropods collected in rock habitat accounting for a higher percentage of gastropods on the Newfoundland Mountains than on Antelope Island (Table 3). Relatively few gastropods were collected in desert shrub in either study area. These distributional patterns among habitat types were also

TABLE 3. Number of gastropods collected from permanent-plot transects, vegetation searches, and soil sifting, May–August 2001 and 2002, on Antelope Island and the Newfoundland Mountains in northern Utah, and number of gastropods infected with protostrongylid-type larvae.

		Habitat type				
	Total collected	Riparian	Rock	Desert shrub	Grass	Total infected
Antelope Island						
2001	335	318	15	0	2	—
2002[a]	980	957	21	1	1	10[b]
Newfoundland Mtns						
2001	53	27	25	1	0	—
2002[a]	227	131	59	7	30	0

[a] All gastropods collected in 2002 were examined for infection by protostrongylid-type larvae.

[b] All infected gastropods were collected in riparian habitat.

reflected in the mean number of gastropods collected per plot on permanent-plot transects (Table 1).

Within each range, the distribution of individual gastropod species differed significantly among habitat types (Antelope Island: $G=14.52$, $P<0.025$; Newfoundland Mountains $G=13.60$, $P<0.005$). On Antelope Island, individual species were primarily concentrated in a particular habitat type (Tables 1 and 2). All of the slugs, most *Vallonia*, and most *Catinella* were encountered in riparian habitat, while *Oreohelix* and *Pupilla* were found most often in rocky habitat. In contrast, *Vallonia* on the Newfoundland Mountains appeared less habitat specific, as it was abundant in both riparian and rock habitats. The unidentified pupillid was collected only in rock habitat on the Newfoundland Mountains.

All live gastropods collected in 2002 were examined for protostrongylid larvae. Ten infected *Vallonia* (1.02% of all gastropods examined from Antelope Island) were found in riparian habitat on Antelope Island; no infected snails were found in any other habitat, or on the Newfoundland Mountains (Table 3). The infected snails accounted for 1.04% of gastropods collected in riparian habitat and 1.3% (10 of 775) of *Vallonia* collected in riparian habitat on Antelope Island in 2002. Mean number of protostrongylid-type larvae per infected *Vallonia* was 4.1±1.8 SE (range=1–19). Six contained L_3 larvae, the stage infective to bighorn sheep, with mean of 2.2±0.8 SE (range=1–6) L_3 larvae. None of the larvae had the dorsal spine characteristic of *P. odocoilei*, however, we could not distinguish among *P. rushi*, *P. stilesi*, *and O. macrotis*.

Bighorn sheep observations

On Antelope Island, 92 ram and nursery groups were observed during May–August 2001 and 2002. Of these, two observations (nursery groups) were not included in the analyses because they occurred in a habitat type not included in this study (recently burned). Twenty-three ram and nursery groups were observed on the Newfoundland Mountains in 2001–02. In 2001, immediately after the introduction, this population used a relatively large portion of the range. However, by 2002 the population remained concentrated in the north part of the range, where the known water sources are located.

Bighorn sheep were observed in all four of the habitat types in which gastropods were collected (Fig. 3). When all observations of bighorn groups within a year were combined, distribution of bighorn sheep among habitat types was significantly different than the distribution of gastropods on both Antelope Island (2001: $G=315.5$, $P<0.001$; 2002: $G=388.8$, $P<0.001$) and the Newfoundland Mountains (2001: $G=9.52$, $P<0.01$; 2002: $G=17.46$, $P<0.001$). On Antelope Island, bighorn sheep were primarily observed in rock and grass habitat types in both years, while the majority of gastropods, *Vallonia* in particular, were collected in riparian habitat (Fig. 3a). In the Newfoundland Mountains in 2001, bighorn sheep were observed only in rock and grass habitat (Fig. 3b). *Vallonia* was abundant in riparian and rock habitat followed by grass habitats. In 2002, bighorn sheep and gastropods were observed in all four habitat types, but the relative abundance of gastropods collected in riparian habitat was higher than the proportion of bighorn observations. Conversely, a high proportion of bighorn sheep observations occurred in desert shrub, where there was a low relative abundance of gastropods.

Between-year differences in distribution of bighorn sheep group types among habitats were not significant (ram: $G=0.80$ $P>0.75$; nursery: $G=0.54$, $P>0.90$), therefore observations for both years on each range were combined by group type to increase statistical power. On Antelope Island, ram and nursery groups were observed in significantly different proportions among the habitat types ($G=11.63$,

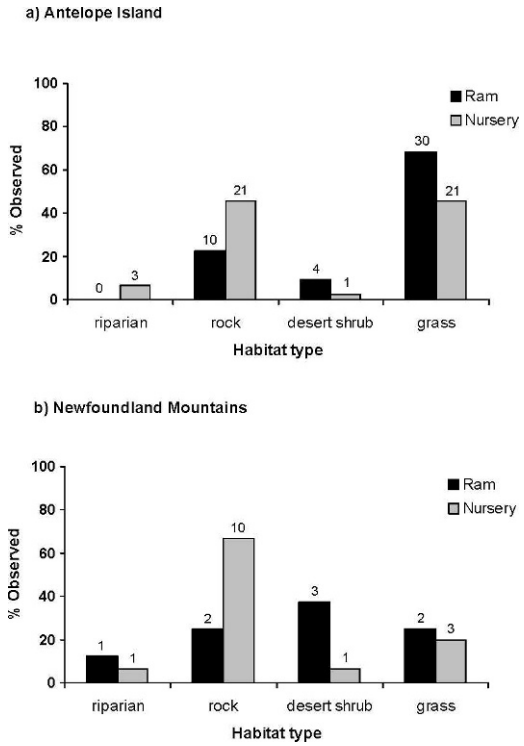

FIGURE 3. Percentage of observations of ram groups and nursery groups in the major habitat types on a) Antelope Island and b) the Newfoundland Mountains, May–August 2001–02. Numbers above bars indicate number of observations.

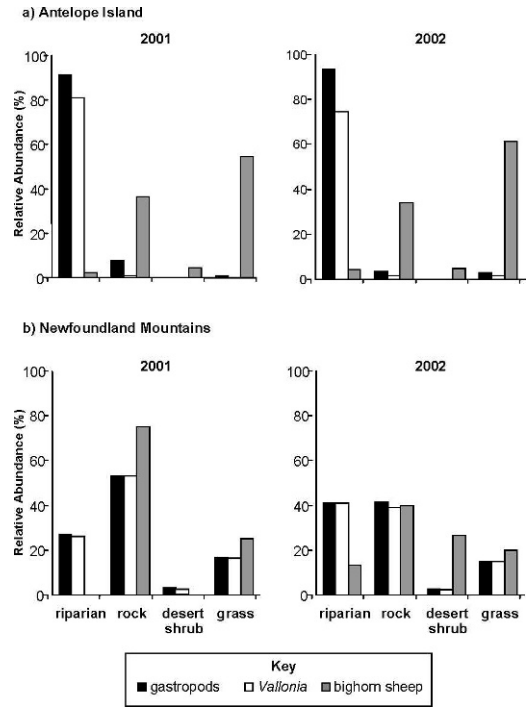

FIGURE 4. Proportions of total gastropods and of *Vallonia* collected in the major habitat types compared with proportion of observations of bighorn sheep groups by habitat type, May–August 2001–02, on a) Antelope Island (2001: $n=335$ total gastropods, 287 *Vallonia*, and 46 groups of bighorn sheep, 2002: $n=980$ total gastropods, 789 *Vallonia*, and 44 groups of bighorn sheep) and b) the Newfoundland Mountains (2001: $n=53$ total gastropods, 53 *Vallonia*, and 8 groups of bighorn sheep, 2002: $n=227$ total gastropods, 223 *Vallonia*, and 15 groups of bighorn sheep).

$P<0.01$; Fig. 4a). Nursery groups were observed in rock habitat more, and grass habitat less, than ram groups. On the Newfoundland Mountains, data suggest that nursery groups may use rock habitat more than ram groups, but differences were not significant ($G=4.905$, $P>0.10$), likely due to small sample size (Fig. 4b).

DISCUSSION

Lungworms (*Protostrongylus* spp. and *Muellerius capillaris*) were considered to be absent from Antelope Island and unlikely on the Newfoundland Mountains prior to the introductions of bighorn sheep. Despite treatment with Ivermectin prior to release on Antelope Island in 1997 and on the Newfoundland Mountains in 2001, a high prevalence of lungworms was observed in bighorn sheep fecal samples collected from the two populations during this study. Ivermectin is not effective against all life stages of lungworms (Easterly et al., 1992; Goldstein et al., 2005). Consequently, lungworms were introduced to these isolated, semiarid ranges with the bighorn sheep. However, all components of the parasite life cycle must be intact on these ranges for transmission and persistence of the parasite.

Although experimental evidence suggests that the *Vallonia*, *Oreohelix*, *Catinella*, and the unidentified slug species on Antelope Island could become infected by protostrongylid larvae (also collected from Antelope Island) and support develop-

ment to L_3 stage (Rogerson, unpublished data), the only gastropods detected with natural protostrongylid infection in this study were *Vallonia* collected from Antelope Island. Prevalence of these infected snails on Antelope Island was only about 1%, while prevalence of lungworms approached 100% in the feces of bighorn sheep. While our method may have underestimated the number of larvae in the gastropods, our results are comparable to other studies. Lungworms were 100% prevalent in bighorn sheep on the Sheep River Wildlife Sanctuary in Alberta, Canada (Festa-Bianchet, 1991a), where prevalence of infected gastropods was 3.8% (Robb and Samuel, 1990). Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer (*Odocoileus virginianus*) in northeastern Minnesota was up to 82% (Slomke et al., 1995), but <1% of gastropods sampled on the range were infected (Lankester and Peterson, 1996).

The high prevalence of lungworm larvae in fecal pellets from lambs established the presence of an intact lungworm life cycle on Antelope Island. Lungworm transmission was not detected on the Newfoundland Mountains during this study, as all 10 fecal samples from lambs collected in 2002 were free of lungworms. On Antelope Island lungworms transferred to fetuses most likely had been recently ingested by the mother because lambs are infected transplacentally with L_3 lungworms (Hibler et al., 1972, 1974; Kistner and Wyse, 1979), which can only reach this infective stage inside an intermediate host. The presence of L_1 lungworms in one of two lamb fecal samples collected on the Newfoundland Mountains in 2001 indicates that the lamb was infected transplacentally by L_3 lungworms acquired by the mother on her former range; Ivermectin administered prior to translocation would have been ineffective at killing sequestered L_3 lungworms (Easterly et al., 1992). In 2002, the negative fecal samples from lambs on the Newfoundland range were collected well past the prepatency period if the lambs had been infected transplacentally from their mothers. On Antelope Island, lungworm larvae were detected in lamb fecal samples as early as 21 May. However, the study may have ended before patent infection developed in lambs that had ingested larvae on the Newfoundland Mountains in mid- to late summer.

Where there is overlap in distributional patterns of intermediate hosts and bighorn sheep, there is potential for lungworm transmission. The most important areas of transmission are likely those with a high abundance of intermediate hosts (Boag and Wishart, 1982; Kralka and Samuel, 1990), but snail activity and bighorn sheep behavior should also be important determinants (Robb and Samuel, 1990). During the summer months on Antelope Island, we suggest that the most probable site of lungworm transmission to bighorn sheep is in riparian habitat, with *Vallonia* as the intermediate host. While low prevalence of infection of other gastropod species in other habitats may have escaped detection, over 90% of all gastropods, and all infected gastropods, collected on the Island were in the riparian habitat type. In addition to containing infective L_3 larvae, snails must be available for ingestion by bighorn sheep, that is, they must be active in the vegetation or soil surface. Only gastropods in riparian habitat were routinely active during the dry summer months (May–August) on both ranges. Though bighorn sheep were rarely observed at springs, fresh bighorn fecal deposits were frequently found in such areas during summer. When groups were observed drinking at springs, they also spent time foraging in the associated vegetation. If *Protostrongylus* spp. establish in the Newfoundland Mountains, riparian habitat also may be an important site of summer transmission there, as well. Although similar gastropod numbers were found in rocks and riparian habitats on the Newfoundland Mountains, gastropods were most active near springs during summer.

While it is possible that transmission of lungworms to bighorn sheep may occur during other seasons (Boag and Wishart, 1982; Robb and Samuel, 1990) in other habitat types, riparian habitat sustains abundant gastropods that are active throughout the year. Springs within, or in proximity to, suitable bighorn habitat would be focal points for visits by bighorn sheep. In nonmigratory populations such as those studied, length of season during which infected gastropods can be ingested may be a critical factor in transmission dynamics. Year-round use of the area by bighorn sheep and the high degree of resistance of L_1 larvae to desiccation and temperature extremes (Forrester and Senger, 1963) suggest that infection of gastropods could occur at any time. Development to L_3 stage in *Vallonia* is temperature-dependent (Samson and Holmes, 1985), but likely occurs faster over a longer season in Utah than in Alberta, Canada. While aestivation of host gastropods slows development of protostrongylid larvae to the infective stage (Solomon et al., 1996), greater activity of gastropods in riparian habitats would lessen this effect on availability of L_3 larvae to bighorn sheep.

On Antelope Island, the median number of L_1 lungworms in bighorn sheep feces was higher for samples from nursery groups than from ram groups. In our study, fecal samples were primarily collected from groups of known composition, but not from known individuals, and therefore may be biased (Wilson et al., 2002); nursery groups often contained a small proportion of young rams ($\leq$2 yr). However, our result of a higher fecal output of L_1 by individuals in nursery groups during lambing season and lactation is consistent with previous work on bighorn sheep (Pelletier et al., 2005) and other ungulates (Gaudernack et al., 1984; Halvorsen et al., 1985) in which fecal outputs were seasonally higher for females than for males. Therefore, because fecal larvae counts of males are typically lower than those of females in early summer, their inclusion with nursery groups makes our result a conservative indication of the difference in larvae counts between the sexes.

Differences in infection levels between groups of individuals may be the result of physiological or ecological mechanisms acting upon individual susceptibility or resistance to parasites (Wilson et al., 2002). Mean intensity of infection with protostrongylid larvae was greater in small rather than large fecal pellets collected from caribou (*Rangifer tarandus caribou*) in Newfoundland, which may reflect immunity-related age factors (Ball et al., 2001). Acquired immunity also may explain the lower fecal output of lungworm larvae by adult bighorn sheep observed in this study and others (Festa-Bianchet, 1991a; Arnett et al., 1993). However, fecal output of lungworms by bighorn sheep $\geq$1 yr was not related to age or body mass (Festa-Bianchet, 1991a; Pelletier et al., 2005).

Other physiological mechanisms proposed to explain differential resistance include differences between sexes in the relationship of stress hormones (e.g., corticosteroids) to immune function (Klein, 2000; Hoby et al., 2006). Levels of fecal glucocorticoid metabolites did not differ between a subherd of bighorn sheep females treated with an anthelmintic to decrease fecal LPG and a control subherd of females, suggesting no relationship between stress hormones and lungworm burdens in female bighorn sheep (Goldstein et al., 2005). Finally, sex differences in parasite susceptibility or resistance may be related to the immunosuppressive effects of sex steroids (Dobson and Meagher, 1996; Hoby et al., 2006) and/or the allocation of energy to reproductive effort in different seasons (Festa-Bianchet, 1989; Pelletier et al., 2005).

The role of ecological mechanisms in sex-biased fecal larvae counts has not been sufficiently addressed, despite sexual segregation being well-documented in bighorn sheep and other ungulates (Main and Coblentz, 1990; Main et al., 1996; Bowyer,

2004). On Antelope Island, distribution of ram and nursery groups differed during the summer, with similar patterns in the Newfoundland Mountain population. In domestic sheep, avoidance of grazing in tall, feces-contaminated patches significantly reduces ingestion of parasite larvae (Cabaret et al., 1986). However, avoidance of these patches is reduced in ewes suckling twins, likely due to the nutritional demands of lactation (Smith et al., 2006). In our study, while neither sex was observed frequently in riparian habitat, sex differences in the use of this habitat type may result in differential ingestion of infected gastropods. Ram groups were observed over a larger range than nursery groups during the summer on Antelope Island (Rogerson, 2003), which may have exposed rams to a lower risk of lungworm transmission via a lower density of bighorns or use of a larger number of water sources resulting in reduced fecal contamination. In addition, rams were observed most often in grass habitat, where few gastropods were collected. Given the prominence of sexual segregation in the annual cycle of bighorn sheep and other species, its role in host-parasite dynamics needs further study (Bowyer, 2004).

Antelope Island and the Newfoundland Mountains supported fewer species of gastropods and at lower abundances than ranges of bighorn sheep in more mesic environments (Latson, 1977; Rowley et al., 1987; Robb and Samuel, 1990). However, our results suggest that although these semiarid climatic conditions may be less favorable for intermediate hosts, the definitive hosts may experience a high level of parasitism. These high levels may be sustained by frequent bighorn use of limited habitat (riparian) that supports healthy gastropod communities, as well as by limited movement of definitive hosts. Although lungworm transmission was not evident on the Newfoundland Mountains during this study, continued monitoring is needed to determine whether *Protostrongylus* spp. eventually become established.

While infection by lungworms was significantly correlated with spring/early summer precipitation in western Montana bighorn sheep (Forrester and Little, 1976), fecal larvae counts were not correlated with spring precipitation in Alberta (Festa-Bianchet, 1991a). On semiarid ranges, water may be an important limiting factor of bighorn sheep distribution. In years of high precipitation, water is available at a greater of number of springs than in drought years. In wet years, bighorn sheep are also less dependent on springs for water because it is available elsewhere through higher moisture content in vegetation and ephemeral pools. In periods of drought, bighorn sheep are dependent on a smaller number of perennial springs, which could result in a greater than normal level of fecal contamination and exposure to infected gastropods in riparian habitats. Thus, a counterintuitive hypothesis suggested by our results is that lungworm infection in bighorn populations on semiarid ranges may increase in dry years, despite the fact that transmission occurs via terrestrial gastropods. This outcome would be dependent, however, on continued ability of perennial riparian habitat to support active snail populations.

The costs and benefits of treating bighorn sheep populations for lungworm should be evaluated and may be indicated only in specific cases (Miller et al., 2000). Our study populations were isolated on habitat islands with little or no opportunity for seasonal migration and high probability of reinfection with lungworms. In addition, the Antelope Island population is frequently used as a source population for reintroductions of bighorn sheep in other parts of Utah. Depending on cost, such situations may make lungworm control desirable. Results from this study suggest that new management strategies involving manipulation of water sources may be developed for controlling lungworm in bighorn sheep populations on semiarid ranges. Reduction of fecal contamination at individual springs might be achieved by developing more water sources for bighorn sheep. Develop-

ment of water sources that can be turned on or off may shift movement patterns of bighorn sheep and may be used to discourage gastropod populations with high prevalence of lungworm infection. Research would be needed to test the effectiveness of these applications.

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